Nature Conservation 16: 1–17 (2016)
doi: 10.3897/natureconservation.16.8604
http://natureconservation.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
Nature Conservation
Launched to accelerate biodiversity conservation

Large-scale coral reef restoration could assist natural recovery in Seychelles, Indian Ocean

Phanor H. Montoya-Maya[1], Kaylee P. Smit[1,2], April J. Burt[1,3], Sarah Frias-Torres[1,4]

1 *Nature Seychelles, Mahe, Republic of Seychelles* **2** *Oceanography Department, Nelson Mandela Metropolitan University (NMMU), Port Elizabeth, South Africa* **3** *Seychelles Islands Foundation, Mahe, Republic of Seychelles* **4** *Smithsonian Marine Station, Fort Pierce, FL, USA*

Corresponding author: *Phanor Hernando Montoya-Maya* (phanor@phmontoyamaya.com)

Academic editor: *I. Sousa-Pinto* | Received 23 March 2016 | Accepted 29 August 2016 | Published 18 November 2016

http://zoobank.org/4BE3FFD6-EBC7-43CA-B9DB-B0AF72949747

Citation: Montoya-Maya PH, Smit KP, Burt AJ, Frias-Torres S (2016) Large-scale coral reef restoration could assist natural recovery in Seychelles, Indian Ocean. Nature Conservation 16: 1–17. doi: 10.3897/natureconservation.16.8604

Abstract

The aim of ecological restoration is to establish self-sustaining and resilient systems. In coral reef restoration, transplantation of nursery-grown corals is seen as a potential method to mitigate reef degradation and enhance recovery. The transplanted reef should be capable of recruiting new juvenile corals to ensure long-term resilience. Here, we quantified how coral transplantation influenced natural coral recruitment at a large-scale coral reef restoration site in Seychelles, Indian Ocean. Between November 2011 and June 2014 a total of 24,431 nursery-grown coral colonies from 10 different coral species were transplanted in 5,225 m^2 (0.52 ha) of degraded reef at the no-take marine reserve of Cousin Island Special Reserve in an attempt to assist in natural reef recovery. We present the results of research and monitoring conducted before and after coral transplantation to evaluate the positive effect that the project had on coral recruitment and reef recovery at the restored site. We quantified the density of coral recruits (spat <1 cm) and juveniles (colonies 1-5 cm) at the transplanted site, a degraded control site and a healthy control site at the marine reserve. We used ceramic tiles to estimate coral settlement and visual surveys with 1 m^2 quadrats to estimate coral recruitment. Six months after tile deployment, total spat density at the transplanted site (123.4 ± 13.3 spat m^{-2}) was 1.8 times higher than at healthy site (68.4 ± 7.8 spat m^{-2}) and 1.6 times higher than at degraded site (78.2 ± 7.17 spat m^{-2}). Two years after first transplantation, the total recruit density was highest at healthy site (4.8 ± 0.4 recruits m^{-2}), intermediate at transplanted site (2.7 ± 0.4 recruits m^{-2}), and lowest at degraded site (1.7 ± 0.3 recruits m^{-2}). The results suggest that large-scale coral restoration may

Copyright *Phanor H. Montoya-Maya et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

have a positive influence on coral recruitment and juveniles. The effect of key project techniques on the results are discussed. This study supports the application of large-scale, science-based coral reef restoration projects with at least a 3-year time scale to assist the recovery of damaged reefs.

Keywords
Reef recovery, coral transplantation, coral settlement, coral recruitment, Acroporidae, Pocilloporidae, Western Indian Ocean

Introduction

A key principle in ecological restoration is to re-establish self-sustaining and resilient ecosystems, similar to their reference ecosystems (Shackelford et al. 2013; Suding et al. 2015). Due to the continued decline of coral reefs worldwide (Hughes 2003; Pratchett et al. 2014), restoration of damaged coral reefs has been recommended as a strategy to assist in reef recovery (Rinkevich 1995, 2008). Restoration of damaged reefs by transplantation of nursery-grown coral colonies increases coral cover, species diversity, coral reproduction capacity and local recruitment (Richmond and Hunter 1990; Horoszowski-Fridman et al. 2011). If donor coral colonies are the survivors of previous bleaching events, coral transplantation increases the spread of bleaching-resistant genotypes and improves resilience (Edwards 2010; Mascarelli 2014). In coral reef restoration, long-term sustainability relies on enhancement of coral recruitment: transplants become an additional source of recruits, or recruits from elsewhere are attracted to the transplanted site by settlement cues associated with the presence of new corals (Kingsford et al. 2002; Sponaugle et al. 2002; Gleason et al. 2009; Dixson et al. 2014).

The 1998 mass coral bleaching event severely affected the reefs of the Indian Ocean (Spencer et al. 2000; Spalding and Jarvis 2002) with 30% mortality recorded at a regional level (Obura 2005). In the Seychelles Archipelago alone, live coral cover decreased to less than 3% in some areas (Graham et al. 2006). Since 1998, recovery has been extremely slow in the inner granitic islands of Seychelles (Graham et al. 2006; Chong-Seng et al. 2014; Harris et al. 2014). Such slow post-bleaching recovery motivated active restoration efforts in the inner Seychelles to assist natural recovery (Frias-Torres et al. 2014). Between November 2011 and June 2014 a total of 24,431 nursery-grown coral colonies from 10 different branching and tabular coral species were transplanted in 5,225 m^2 (0.52 ha) of degraded reef at the no-take marine reserve of Cousin Island Special Reserve (Frias-Torres et al. 2014; Frias-Torres and van de Geer 2015; Frias-Torres et al. 2015).

Could coral transplantation have a positive effect on coral recruitment and therefore enhance reef recovery at the restored site? Coral recruitment did not change when comparing sites with coral settlement structures with and without coral transplants (Maldives, Clark and Edwards 1995) or comparing with untouched control areas (Indonesia, Ferse et al. 2013). Both studies recommended coral transplantation as a last resort when reef recovery is hindered due to limited natural recruitment. When coral fragments were transplanted directly to the natural reef substrate, coral recruitment in transplanted areas

was higher than in denuded non-transplanted areas (Tanzania, Mbije et al. 2013). From these studies it is unclear whether coral transplantation is effective in enhancing natural coral recruitment or in accelerating reef recovery. Such uncertainty hinders the cost-effectiveness of ongoing and future coral transplantation projects. A possible limitation in our understanding of the effectiveness of coral transplantation is due to the small scale of transplant studies (<0.1 ha) compared to the scale of reef damage, because the transplantation of nursery-reared colonies to a degraded reef at small scales might be insufficient to enhance local coral recruitment (Edwards and Gomez 2007).

Our aim was to evaluate the effects of large-scale coral restoration on coral recruitment in a no-take marine reserve. We assessed the spatial differences in natural coral recruitment and juveniles after coral transplantation. We quantified coral recruitment and juveniles at the transplanted site and two untouched sites: healthy and degraded. The healthy and degraded sites served as a reference for natural coral recruitment. We hypothesized that coral recruitment and juveniles would be highest at the healthy site, intermediate at the transplanted site, and lowest at the degraded site. This study will contribute to our understanding of the effectiveness of large-scale coral restoration in enhancing natural coral recruitment or in accelerating reef recovery.

Methods

Study site

The study site was a continuous fringing reef on the south-west side of Cousin Island (Figure 1). The reef is approximately 400 m long and 30 m wide (ca. 1.2 ha), ranging in depth between 6.5 and 13 m. Corals of a 40 m long section of the reef at its southernmost end (4°20'09"S, 55°39'32"E) survived the 1998 mass coral bleaching event. This survivor section became the healthy site (ca. 0.12 ha), one of the untouched reference sites. Coral cover in this section of the reef has shown good recovery from <15% in 2012 to <35% in 2014 (Figure 1), and is dominated by *Acropora* (e.g. *A. appressa*, *A. cytherea*, *A. humilis*, *A. hyacinthus*) and *Pocillopora* (*P. grandis* and *P. verrucosa*) species. Coral cover in the remainder of the reef (ca. 1 ha) was less than 3%. Here, a 50-m long section of the reef, north-west (4°20'08"S, 55°39'30"E) of the healthy site, was selected as the degraded site (ca. 0.13 ha), the other untouched reference site, where a mix of consolidated, unconsolidated rubble and sand dominate the substrate, and coral cover has remained unchanged since 2012 (Figure 1). A 150-m long section of the degraded reef north (4°20'04"S, 55°39'25"E) of the degraded site was targeted for restoration through coral transplantation. This was the transplanted site (0.52 ha), where the substrate resembled the degraded site in 2012. Although 10 different branching/tabular species were transplanted in this site (*Acropora cytherea*, *A. damicornis*, *A. formosa*, *A. hyacinthus*, *A. abrotanoides*, *A. lamarki*, *A. vermiculata*, *Pocillopora damicornis*, *P. indiania, P. grandis* and *P. verrucosa*; species identification after Veron 2000 and nomenclature after the World Register of Marine Species [www.marinespecies.org]),

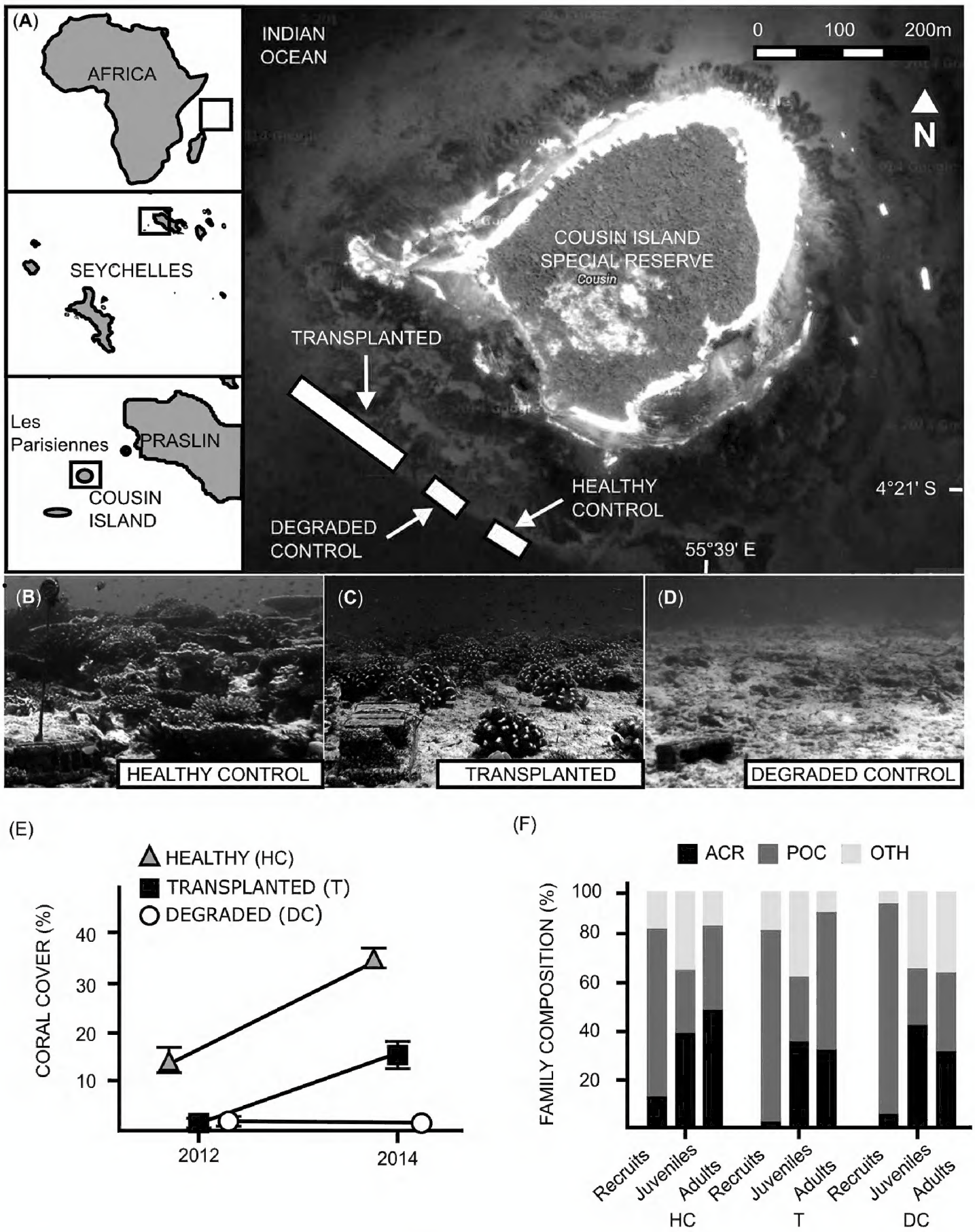

Figure 1. Study area and live coral cover and family composition at each site. **A** Locations of Seychelles, Cousin Island, donor site (Les Parisiennes) and the three study sites: healthy control, degraded control and transplanted. Lower panel shows the seascape and concrete blocks with tiles at **B** healthy control (HC) **C** transplanted (T) and **D** degraded control (DC) sites. **E** Change in average (± SE) live coral cover (% of total area) for individual sites between the start (November 2012) and the end (June 2014) of the transplantation project. **F** Family (ACR = Acroporidae; POC = Pocilloporidae; OTH = Other families) composition (% of total coral species) at three different stages (i.e. recruits, juveniles and adults) of the life cycle of corals in the three study sites at the end of sampling period. No significant differences in juveniles composition between sites or sampling periods were found.

the dominant transplanted coral genus was *Pocillopora,* which included one broadcast spawner (*P. grandis*) and two facultative brooding (*P. verrucosa* and *P. damicornis*) species (Schmidt-Roach et al. 2012 and references therein). All three study sites were separated by arbitrarily defined 50-m buffer zones. Figure 1 shows the 2012 and 2014 coral cover as well as the 2014 coral family composition for each site.

Our experience in the local conditions indicated strong (~0.5 m s^{-1}) bidirectional currents along the reef with no clear seasonal pattern due to local winds, tides and bathymetry (Jennings et al. 2000). From May to October the trade winds blow from the southeast (Southeast Monsoon), and from December to March they tend to blow from the northwest (Northwest Monsoon). The transition months of April and November have light and variable winds. The current and wind conditions suggest that all sites were equally exposed to two major environmental factors that affect coral settlement and recruitment, namely current patterns and connectivity to sources of coral larvae. We recognize that the differential post-1998 bleaching survivorship of the study area may suggest variations in microhabitat and small-scale oceanographic conditions between sites. However, we considered that any differences in environmental conditions between the transplanted and degraded sites were negligible because these two sites were similarly affected by the 1998 coral bleaching event and remained equally degraded prior to the start of the coral transplantation project in November 2011 (Figure 1). Further, Chong-Seng et al (2014) found that rates of coral recruitment to settlement tiles were similar across three different reef conditions (coral-dominated, rubble-dominated, and macroalgal-dominated reefs) in the inner Seychelles, suggesting that larval supply is not a limiting factor for reef recovery. Therefore, we assumed all three sites had the same likelihood of receiving coral larvae.

Coral recruitment

We deployed settlement tiles onto the reef between 9th and 15th January 2014, over 14 months after first coral transplantation. Based on our coral reproduction monitoring, this deployment schedule allowed approximately 3 weeks biological conditioning of the tiles prior to the first expected coral spawning in the area, the first week of February 2014 (Montoya-Maya, unpublished data).

Coral recruitment (spat <1 cm) was compared among all three study sites over a six-month period using settlement tiles. Two ceramic tiles (16 × 16 × 0.8 cm) were placed separately on a concrete block and secured with a plastic cable tie. Flat ceramic tiles attached to concrete blocks were used, rather than other more efficient coral settlement methods (e.g. tiles of differing texture and orientation; Petersen et al. 2005), due to the difficulty of sourcing local materials for more complex settlement structures. Although the results could provide an underestimate of total coral recruitment rates, we considered tile placement appropriate for our objectives. In January 2014, 20 concrete blocks, with two tiles per block, were deployed at each of the three study sites. All concrete blocks were deployed within the same depth range (8–10 m) with adjacent blocks

separated by 5 m. This deployment setup resulted in comparable survey areas (ca. 0.12 ha) at each site despite the transplanted site being larger. Tiles were retrieved in July 2014, >19 months after first transplantation. Tiles were left to dry in the sun for 24 hours and then rinsed in freshwater to remove sediments. Biofouling was insignificant and similar across sites, therefore, we considered unnecessary soaking the tiles in diluted bleach. Each tile was then visually examined twice by different observers using a stereomicroscope to identify coral spat. The coral spat were counted and identified to family level. Families of newly settled corals were identified following Babcock et al. (2003). Families that could not be identified due to damage or insufficient development were pooled into the category "unidentified".

Coral juveniles

Coral juveniles were assessed four times: before transplantation, 12, 18 and 24 months after first transplantation. Abundance and diversity were quantified at genus level for coral juveniles by SCUBA diving and counting the number of juvenile scleractinian corals (<5 cm in diameter) within 1 m^2 quadrats on natural substrate. At the transplanted, degraded and healthy sites, six 10-m transects were deployed and within each transect three quadrats were randomly placed (using a random number table) for juvenile coral abundance. The substratum of each quadrat was carefully examined for non-fragmented small colonies. Any obstructive macroalgae was parted when necessary. Colonies resulting from fission, shrinkage or fragmentation of older colonies were excluded. Because individual corals were not being monitored through time and fixed quadrats were not used, estimates were considered as total number of juveniles (i.e. new juveniles and old juveniles) and not as an estimate of recruitment rates (i.e. number of new recruits per unit time).

Statistical analysis

The experimental design we used was a compromise between scientific objectives and the time required to implement a large-scale coral reef restoration project. We acknowledge the limitations such an approach has in our ability to statistically test the effect of the coral transplantation effort. Accordingly, differences in recruit and juvenile density between the three sites were evaluated using generalized linear mixed models (GLMMs) with a Poisson error structure, with the log link function and site as a fixed effect. There were two types of random factors. In recruit density, we used tile nested within cement block to account for pseudo replication. In juvenile density, we used time and quadrat nested within transects to account for pseudo replication and irregular monitoring intervals. We used the likelihood radio (LR) test to determine the influence of fixed and random effects on recruit and juvenile densities by comparing the fit for models with and without the conditions (Bolker et al. 2009). When over-dispersion and excess of zeros were present in the data, a quasi-Poisson count variance structure with zero-inflated

models was used (Bolker et al. 2009; Harrison 2014). We completed the analyses for each of the two main transplanted families separately (Acroporidae and Pocilloporidae), for all other families pooled, and for all taxa pooled. All statistical tests were done in R (R Core Team 2013), for fitting GLMMs the *lme4* (v1.1-6: Bates et al. 2014) and *glmmADMB* (v0.8.0: Skaug et al. 2012) packages were used.

Results

Coral recruitment

During the six-month study, 326 spat were counted across all sites: 192 (58.9%) recruited on the upper surface of the tile and 134 (41.1%) settled on the sides. Pocilloporid corals predominated at all sites (80.7% of recruits) followed by other families (13.5%) and Acroporidae (5.8%). The average density was 2.8 ± 0.19 spat $tile^{-1}$ (86 ± 6.1 spat m^{-2}) and ranged from 0 to 13 spat $tile^{-1}$ (0 - 351.4 spat m^{-2}). Although the contribution of Pocilloporidae to the total number of spat at each site varied slightly (71.6-89.9%), the contribution of Acroporidae at the healthy site (12.6%) was higher than transplanted site (2.0%; Figure 1).

Total recruitment varied significantly among sites (LR test: $\chi^2 = 15.50$, $df = 2$, $P < 0.001$) and similar results were found for the three coral taxa examined (Acroporidae: $\chi^2 = 6.77$, $df = 2$, $P = 0.034$; Pocilloporidae: $\chi^2 = 11.2$, $df = 2$, $P = 0.004$; Other families: $\chi^2 = 12.10$, $df = 2$, $P = 0.002$). Spat density at the transplanted site was 1.6 times (0.46 ± 0.15, β ± SE on the logit scale; Figure 2) higher than the healthy site (GLMM, $z = 3.15$, $P = 0.002$; Table 1). Pocilloporid spat density at the transplanted site was 1.8 times higher (0.58 ± 0.18, on the logit scale; Figure 2) than the healthy site (GLMM, $z = 3.20$, $P < 0.01$). Although degraded site had consistently lower spat densities for all taxa examined, spat density from other than the two dominant families at the degraded site was significantly lower than the healthy site (GLMM, $z = -2.15$, $P < 0.05$; Figure 2). Spat density at the transplanted site was higher than the degraded site for pocilloporids (GLMM, $z = 2.52$, $P = 0.012$), other coral families (GLMM, $z = 3.12$, $P = 0.002$), and all taxa combined (GLMM, $z = 3.68$, $P < 0.001$), between 1.6 (Pocilloporidae) to 6 (Other families) times higher than degraded site (Table 1).

Coral juveniles

Throughout the four sampling periods between November 2012 and October 2014, 527 juveniles were counted in 216 quadrats. The overall juvenile density was 3.1 ± 0.19 juveniles m^{-2}, ranging from 0 to 16 recruits m^{-2}. Acroporid juveniles were 40.2% of the total coral juveniles across sampling periods, followed by other families (37.2%) and Pocilloporidae (22.6%). The family distribution of coral juveniles was similar between sampling periods and between study sites (Figure 1).

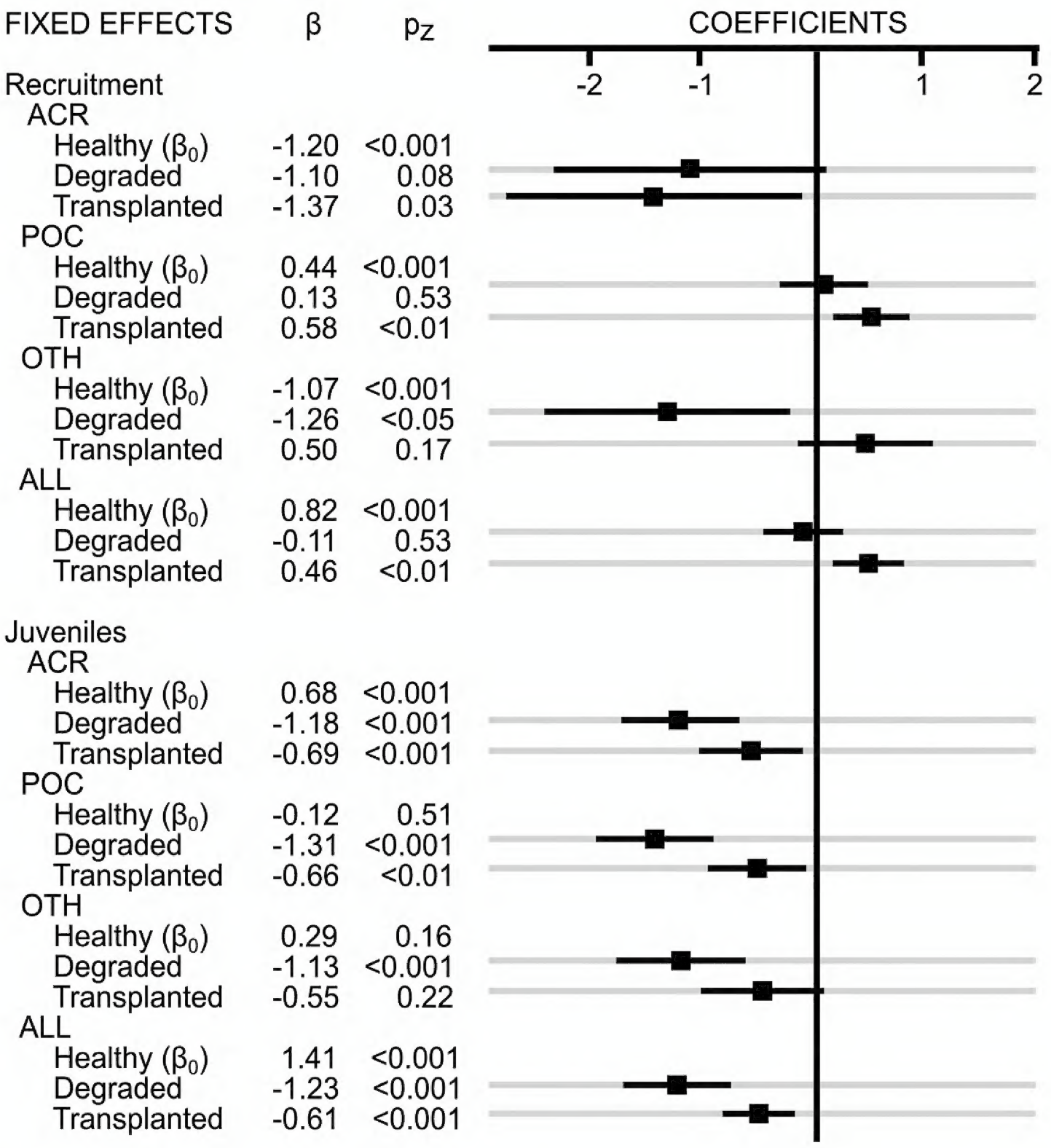

Figure 2. Estimated influence (marker) and 95% confidence intervals (lines) of each study site (DC– degraded control; HC – healthy control; T – transplanted) on coral recruitment and juveniles of acroporidae (ACR), pocilloporidae (POC), other coral families (OTH), and all individuals combined (ALL) based on poisson- distributed generalized linear mixed effect models (GLMMs). The HC site was set as the reference level (intercept). *A quasi-Poisson distribution family was set in the model to account for over dispersion.

Total juveniles varied among sites ($\chi^2 = 35.13$, $df = 2$, $P < 0.001$) and similar results were obtained for the three coral taxa examined (Acroporidae: $\chi^2 = 27.69$, $df = 2$, $P < 0.001$; Pocilloporidae: $\chi^2 = 23.48$ $df = 2$, $P < 0.001$; Other families: $\chi^2 = 18.73$, $df = 2$, $P < 0.001$). The healthy site had the highest total juvenile density (GLMM, $z = 6.74$, $P < 0.001$; Table 1), particularly of Acroporidae (GLMM, $z = 3.34$, $P < 0.001$; Figure 2). The

Table 1. Estimates of spat and juvenile densities (mean ± SE) of Acroporidae, Pocilloporidae, other coral families (Other) and all families combined (All taxa) for each study site.

Taxon	Healthy Control	Degraded Control	Transplanted
Acroporidae			
Spat tile^{-1}	0.3 ± 0.08	0.1 ± 0.06	0.1 ± 0.04
Spat m^{-2}	9.7 ± 2.61	3.3 ± 1.95	3.3 ± 1.30
Juvenile m^{-2}	2.1 ± 0.24	0.7 ± 0.16	1.0 ± 0.19
Pocilloporidae			
Spat tile^{-1}	1.7 ± 0.22	1.9 ± 0.22	3.1 ± 0.43
Spat m^{-2}	55.4 ± 7.17	61.9 ± 7.20	101.0 ± 14.01
Juvenile m^{-2}	1.4 ± 0.18	0.4 ± 0.09	0.6 ± 0.11
Other			
Spat tile^{-1}	0.4 ± 0.04	0.1 ± 0.06	0.6 ± 0.13
Spat m^{-2}	13.0 ± 1.30	3.3 ± 1.95	19.5 ± 4.23
Juvenile m^{-2}	1.6 ± 0.16	0.5 ± 0.11	1.1 ± 0.21
All taxa			
Spat tile^{-1}	2.1 ± 0.24	2.4 ± 0.22	3.8 ± 0.41
Spat m^{-2}	68.4 ± 7.82	78.2 ± 7.17	123.8 ± 13.35
Juvenile m^{-2}	4.8 ± 0.40	1.7 ± 0.26	2.7 ± 0.38

Recruitment is expressed as both spat tile^{-1} and no. spat m^{-2}. The latter represent standardized units.

degraded site had the lowest total juvenile density (GLMM, $z = -6.36$, $P < 0.001$; Figure 2), particularly of Pocilloporidae (GLMM, $z = -5.06$, $P < 0.001$; Figure 2). Juvenile density at the transplanted site was consistently higher than the degraded site (Acroporidae: GLMM, $z = 2.06$, $P = 0.039$; Pocilloporidae: GLMM, $z = 2.36$, $P = 0.019$; other families: GLMM, $z = 2.12$, $P = 0.034$; all taxa: GLMM, $z = 3.10$, $P < 0.01$; Figure 3), between 1.1 (Acroporidae) to 1.9 (Pocilloporidae) times higher than degraded site (Table 1). The time of sampling period had a significant influence on the juvenile density of all taxa ($\chi^2 = 10.28$, $df = 1$, $P < 0.01$) and Acroporidae ($\chi^2 = 6.83$, $df = 1$, $P < 0.01$); likely driven by a higher count of juveniles at the end of this study (Figures 3 and 4). However, the influence of sampling period on juvenile density was not statistically significant for Pocilloporidae ($\chi^2 = 0.55$, $df = 1$, $P = 0.457$) and other coral families ($\chi^2 = 1.94$, $df = 1$, $P = 0.164$).

Discussion

We quantified spatial differences in natural coral recruitment and juveniles after large-scale coral transplantation by comparing two untouched control sites (healthy and degraded) with the transplanted site. Coral recruitment was assessed >14 months after first transplantation using a single tile deployment. Six months after tile deployment, total spat density at the transplanted site was 1.8 times higher than the healthy site and 1.6 higher than the degraded site, but the magnitude of variation in coral recruitment between the transplanted site and the degraded site was up to 6 times for coral families other than Pocilloporidae and Acroporidae. Spatial variation in early coral

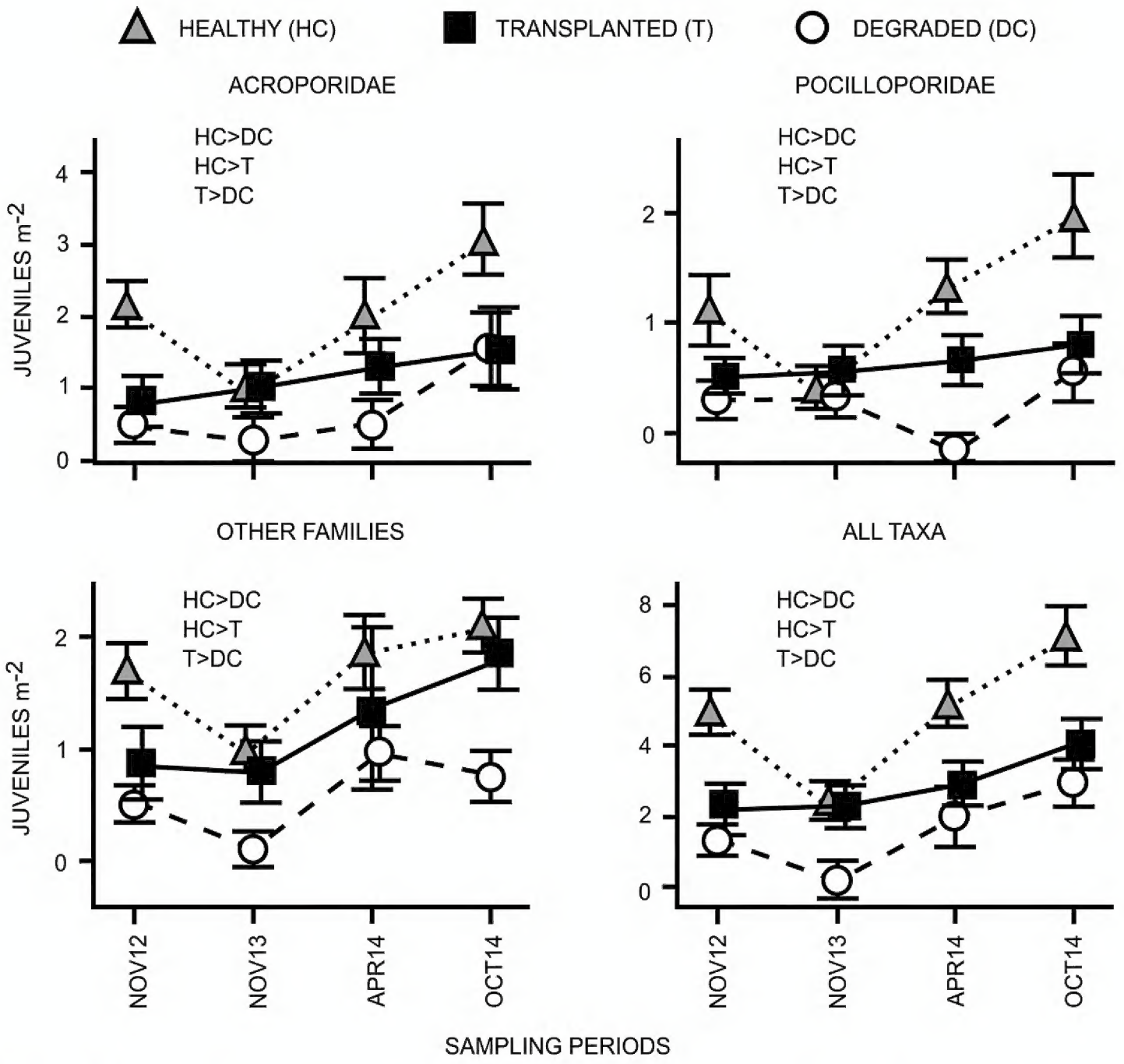

Figure 3. Mean (±SE) numbers of juveniles observed at the three study sites by sampling period. Data are presented for all individuals combined and for Acroporidae, Pocilloporidae and other families separately. Dates correspond to the four sampling periods. Statistical significant differences ($P < 0.05$) between sites are also shown.

recruitment is common between and within reefs (Fisk and Harriot 1990; O'Leary and Potts 2011). The variation at larger scales has been explained by differences in habitat quality, represented by differences in adult cover and substrate composition (Vermeij 2005), whereas at smaller scales it has been related to fish grazing and predation (O'Leary and Potts 2011). Coral transplantation clearly results in the modification of coral cover and substrate composition at the transplanted site (Edwards and Gomez 2007; Frias-Torres et al. unpublished data). Therefore, it is possible that the changes in habitat quality resulting from large-scale coral transplantation promote coral recruitment at the transplanted site.

We propose three reasons to explain the increase in coral recruitment at the transplanted site. First, the transplanted corals increase local production of coral larvae.

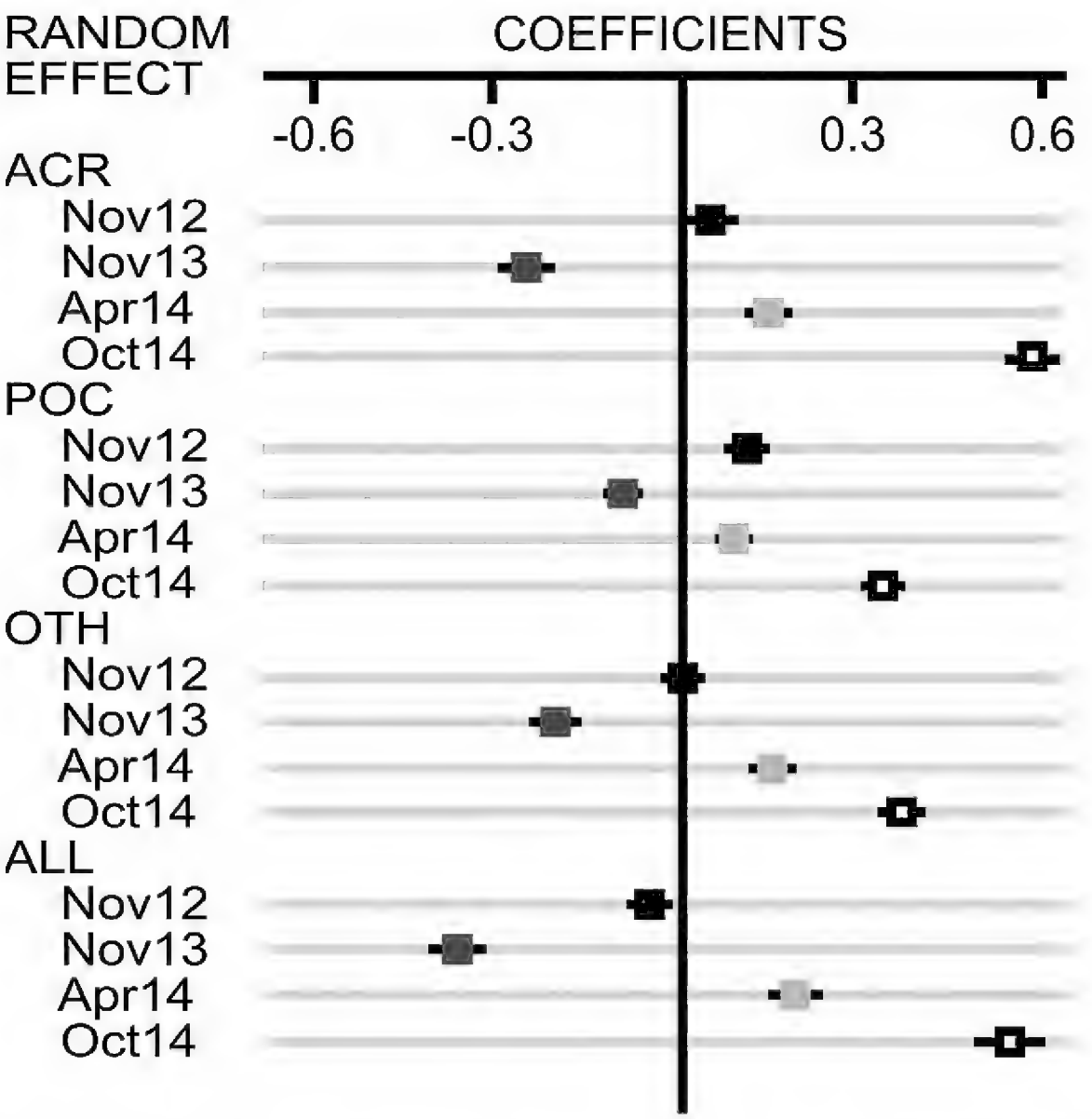

Figure 4. Estimates of the effects of sampling period on coral juveniles across the three sampled sites. Estimated coefficient (marker) and 95% confidence intervals (lines) are shown for all individuals combined (ALL) and for acroporidae (ACR), pocilloporidae (POC) and other families (OTH) separately.

The transplanted colonies were large enough at transplantation time (>15 cm) to have a high probability of being mature (Babcock 1991; Montoya-Maya et al. 2014) and there were gravid colonies at the transplanted and healthy sites (P. H. Montoya Maya, personal communication, February 2014). It is possible that the majority of larvae settling at the transplanted site were locally produced by the dominant transplanted coral genus *Pocillopora*. This genus included brooding species with larvae that can settle very close to parental colonies (Gorospe and Karl 2013). Second, the transplanted site attracts more coral larvae from elsewhere due to an increase in settlement cues. The transplanted site has an area three times larger than the two control sites (Figure 1), high species diversity and coral cover. These conditions may offer more available space and signal more favorable settlement, survival and growth conditions to incoming coral larvae (Kingsford et al. 2002; Sponaugle et al. 2002; Vermeij 2005; Edwards and Gomez 2007; Suzuki et al. 2008; Nakamura and Sakai 2009; Dixson et al. 2014) compared to the healthy and degraded sites. The higher recruitment of acroporids at the healthy site and of pocilloporids at the transplanted site - where their respective

coral cover (Figure 1) and adult densities are higher (Frias-Torres et al. unpublished data) – also add support to this statement. The lower number of total recruits at the healthy site, where coral structure is better, may be explained by an increase in recruit mortality from fish predation and grazing (O'Leary and Potts 2011) due to having a more diverse fish community than the two other sites (Frias-Torres et al. unpublished data). Further, a positive relationship between adult cover and recruitment rates (spat $tile^{-1}$) was found for pocilloporids in the Inner Seychelles (Chong-Seng et al. 2014). Enhanced settlement cues at the transplanted site due to the large-scale nature of the restoration project explain the overall higher number of coral spat and the higher number of spat from non-transplanted families compared to the degraded site. Third, both self-recruitment and attraction from elsewhere increased overall recruitment at the transplanted site. Such interaction of self-recruitment and attraction to increase coral recruitment has been suggested at a previous coral restoration study in Kenya (Mbije et al. 2013). We suggest future research could use techniques to identify immigrant and locally produced spat (e.g. assignment tests, Broquet and Petit 2009) to determine the real effect coral transplants have in local seeding or larval attraction from elsewhere.

Coral juveniles were assessed over a 2-year period that included sampling before and after coral transplantation. Total juvenile density and that of the three taxa examined was highest at the healthy site, intermediate at the transplanted site and lowest at the degraded site. Juvenile density at the transplanted site was consistently higher than the degraded site: between 1.1 (Acroporidae) to 1.9 (Pocilloporidae) times higher. Structural complexity is related to higher recovery rates due to enhanced recruit survival (e.g. indirectly reduces competition with algae and erosion by urchins or loose rubble; Graham and Nash 2013). This explains the higher recruit density at the healthy site (high structural complexity) compared to the transplanted site (medium structural complexity) and the higher juvenile density of the healthy and transplanted sites compared to the degraded site (low structural complexity; Jörgensen et al 2015). Similar results were obtained when comparing coral recruitment between high-, intermediate-, and low-quality zones in Florida (Vermeij 2005). Alternatively, natural recovery of the reefs in the inner Seychelles is ongoing (see Graham et al 2015) and the healthy site compared to the other two sites is leading the way as it is an "older" reef which has been accumulating small corals for longer. Nevertheless, coral transplantation may help in accelerating natural recovery of a degraded reef by improving its structural complexity. This will explain the differences in the number of coral juveniles between the transplanted and degraded sites, and the steady uptrend in the density of coral juveniles at the transplanted site over the sampling period when compared to the other two sites. Therefore, physical (e.g. varying sizes and growth forms of coral transplants on sites) and biological (e.g. including fish, snails and any other reef organism known to help coral recruit survival) complexity should be promoted in reef restoration projects to enhance the survival of settlers (Biggs 2013). In addition, in future studies it would be valuable to include a measure of complexity (e.g. rugosity) to evaluate coral settlement and recruitment on transplanted sites with varying levels of structural complexity.

The healthy-degraded-transplanted site cluster lacks replication at multiple locations and multiple times which limits the generalization of our results (Underwood 1993). Therefore, other alternative explanations to our results should be considered. One alternative is that the differences observed in coral settlement and recruitment among the sites existed prior to coral transplantation. A second alternative to consider is differential larval supply to the three sites. Although the sites are part of a single fringing reef, the healthy and transplanted sites are located at opposite ends of the reef which could result in differences in connectivity to source reefs. We found these two alternatives unlikely because there were similar estimates of coral spat between the two reference sites and there were similar number of juveniles between the transplanted and degraded sites before transplantation. In addition, coral juveniles at the transplanted site showed a constant uptrend in contrast to the up- and downtrend seen at the healthy and degraded sites (Figure 3). Finally, spatial variation in coral settlement and recruitment in the inner Seychelles has not been linked to differences in larval supply, which results in similar rates of coral settlement between reefs of different habitat quality (Chong-Seng et al. 2014). The lack of replication in our study hinders our ability to rule out completely all alternative explanations. We found the most parsimonious interpretation is that the transplantation of nursery-grown corals onto the degraded site resulted either in the attraction or the production (or both) of more coral larvae than the two control sites (healthy and degraded), with a higher chance of survival of settled corals at the transplanted site than at the degraded site. Even with its limitations, this study shows that the large-scale coral restoration effort in Seychelles assisted the natural recovery of the transplanted reef.

Our results are consistent with conclusions and best practices outlined in previous studies of coral reef restoration for species selection and transplant substrate. The use of brooding species in reef restoration projects is seen as a particularly effective form of transplantation (Rinkevich 1995; Edwards and Clark 1999). Our high spat density from the dominant transplanted family, Pocilloporidae, supports this. We cemented coral transplants directly onto denuded reef areas without the use of artificial structures, which allowed corals to self-attach 1-2 months post-cementing. Such technique may have increased survival of coral transplants, which further enhanced coral settlement and recruitment. Similar results were obtained by Mbije et al (2013) in Tanzania when transplanting corals onto denuded reefs without the use of artificial structures. Artificial structures in reef restoration projects increase transplant mortality due to their instability and the shorter lifespan of the structure (Clark and Edwards 1995; Ferse et al. 2013), and decrease abundance and diversity of coral recruits at restoration sites (Biggs 2013).

The effects of project size, duration and location should also be considered. Increasing the size of the transplanted area and expanding the monitoring time are required to observe any positive effects of active reef restoration (Edwards and Gomez 2007; Normile 2009). The number of corals and size of area transplanted make our project the largest reef restoration effort completed to date (Clark and Edwards 1995 Ferse et al. 2013; Mbije et al. 2013). An upward trend in coral recruitment was evident in our study with modeled coefficients of time effects consistently higher 24 months

after transplantation. Similar results were observed by Ferse et al. (2013) 14 months after transplantation in Sulawesi, Indonesia, for settlement of Acroporidae and Pocilloporidae. It is possible that previous projects were too small to cause a positive influence on coral recruitment, or the monitoring time period was too short to observe any effects. Project location is critical to detect the signal of increased coral settlement and recruitment. Our project was carried out within a no-take marine reserve where human stressors that can interfere with natural reef recovery were controlled. Therefore, our results support the application of large-scale, science-based coral reef restoration projects with at least a three year monitoring time-scale to assist the recovery of damaged reefs within protected areas.

Our approach confirmed the hypothesis that scleractinian coral recruitment and juveniles will be higher at the transplanted site than at the degraded site. As coral reefs continue to degrade, it is imperative that we understand how active reef restoration impacts natural reef recovery. We have shown coral transplantation with colonies large enough to be reproductive results in higher structural complexity, self-recruitment and recruitment of non-transplanted species. These results confirm coral reef restoration can be sustainable in the long-term. Enhanced natural coral settlement and recruitment resulting from coral transplantation holds great promise for the success and long-term sustainability of large-scale coral reef restoration, at least for those projects aimed at assisting the recovery of naturally degraded reefs in the Seychelles.

Acknowledgements

We thank S. Beach, S.C. Klaus, E. Martin, C. Reveret, K. Rowe and N. Taylor for help during fieldwork. N. Shah and K. Henri at Nature Seychelles for managing the Reef Rescuers Project. A. Hennie from Black Pearl Seychelles, for allowing us to use their stereomicroscope. Several anonymous reviewers gave constructive criticisms improving the manuscript. Funding to Nature Seychelles was received through the United States Agency for International Development (USAID) Reef Rescuers Project 674-A-00-10-00123-00.

References

Babcock RC (1991) Comparative demography of three species of scleractinian corals using age- and size- dependent classifications. Ecological Monographs 61(3): 225–244.

Babcock RC, Baird AH, Piromvaragorn S, Thomson DP, Willis BL (2003) Identification of scleractinian coral recruits from Indo-Pacific Reefs. Zoological Studies 42(1): 211–226.

Bates D, Mächler M, Bolker BM, Walker SC (2014) Fitting Linear Mixed-Effects Models using lme4. Journal of Statistical Software 51 pp.

Biggs BC (2013) Harnessing Natural Recovery Processes to Improve Restoration Outcomes: An Experimental Assessment of Sponge-Mediated Coral Reef Restoration. PLoS ONE 8(6): e64945. doi: 10.1371/journal.pone.0064945

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JS (2009) Generalized Linear Mixed Models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24(3): 127–135. doi: 10.1016/j.tree.2008.10.008

Broquet T, Petit EJ (2009) Molecular estimation of dispersal for ecology and population genetics. Annual Reviews of Ecology, Evolution and Systematics 40(1): 193–216. doi: 10.1146/annurev.ecolsys.110308.120324

Chong-Seng KM, Graham NAJ, Pratchett MS (2014) Bottlenecks to coral recovery in the Seychelles. Coral Reefs 33(2): 449–461. doi: 10.1007/s00338-014-1137-2

Clark S, Edwards AJ (1995) Coral transplantation as an aid to reef rehabilitation: evaluation of a case study in the Maldive Islands. Coral Reefs 14(4): 201–213. doi: 10.1007/BF00334342

Dixson DL, Abrego D, Hay ME (2014) Chemically mediated behavior of recruiting corals and fishes: a tipping point that may limit reef recovery. Science 345(6199): 892–897. doi: 10.1126/science.1255057

Edwards AJ (2010) Reef rehabilitation manual. Coral Reef Targeted Research and Capacity Building for Management Program. St Lucia, 166 pp.

Edwards AJ, Clark S (1999) Coral transplantation: a useful management tool or misguided meddling? Marine Pollution Bulletin 37(8/12): 474–487. doi: 10.1016/S0025-326X(99)00145-9

Edwards AJ, Gomez ED (2007) Reef restoration concepts and guidelines: making sensible management choices in the face of uncertainty. Coral Reef Targeted Research and Capacity Building for Management Programme, St Lucia, 38 pp.

Ferse SCA, Nugues MM, Romatzki SBC, Kunzmann A (2013) Examining the use of mass transplantation of brooding and spawning corals to support natural coral recruitment in Sulawesi/Indonesia. Restoration Ecology 21(6): 745–754. doi: 10.1111/rec.12004

Fisk DA, Harriott VJ (1990) Spatial and temporal variation in coral recruitment on the Great Barrier Reef: Implications for dispersal hypotheses. Marine Biology 107(3): 485–490. doi: 10.1007/BF01313433

Frias-Torres S, van de Geer C (2015) Testing animal-assisted cleaning prior to transplantation in coral reef restoration. PeerJ 3: e1287. doi: 10.7717/peerj.1287

Frias-Torres S, Rowe K, Reveret C (2014) Reef Rescuers: restoring reefs in the face of climate change. Nature Seychelles Quarterly Progress Report No. 14 (April-June 2014). Unpublished Report to Nature Seychelles. United States Agency for International Development (USAID) Project 674-A-00_10-001. 22 pp.

Frias-Torres S, Goehlich H, Reveret C, Montoya-Maya PH (2015) Reef fishes recruited at midwater coral nurseries consume biofouling and reduce cleaning time in Seychelles, Indian Ocean. African Journal of Marine Science 37(3): 421–426. doi: 10.2989/1814232X.2015.1078259

Gleason DF, Danilowicz BS, Nolan CJ (2009) Reef waters stimulate substratum exploration in planulae from brooding Caribbean corals. Coral Reefs 28(2): 549–554. doi: 10.1007/s00338-009-0480-1

Gorospe KD, Karl SA (2013) Genetic relatedness does not retain spatial pattern across multiple spatial scales: dispersal and colonization in the coral, *Pocillopora damicornis*. Molecular Ecology 22: 3721–3736.

Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef ecosystems. Coral Reefs 32(2): 315–326. doi: 10.1007/s00338-012-0984-y

Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518: 94–97.

Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. Proceedings of the National Academy of Sciences of the United States of America 103(22): 8425–8429. doi: 10.1073/pnas.0600693103

Harris A, Wilson S, Graham NAJ, Sheppard C (2014) Scleractinian coral communities of the inner Seychelles 10 Years after the 1998 Mortality Event. Aquatic Conservation 24(5): 667–679. doi: 10.1002/aqc.2464

Harrison XA (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution. PeerJ 2: e616. doi: 10.7717/peerj.616

Horoszowski-Fridman YB, Izhaki I, Rinkevich B (2011) Engineering of coral reef larval supply through transplantation of nursery-farmed gravid colonies. Journal of Experimental Marine Biology and Ecology 399(2): 162–166. doi: 10.1016/j.jembe.2011.01.005

Hughes TP (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301(5635): 929–933. doi: 10.1126/science.1085046

Jennings S, Marchall SS, Cuet P, Naim O (2000) The Seychelles. In: McClanahan TR, Sheppard CRC, Obura DO (Eds) Coral Reefs of the Indian Ocean: Their Ecology and Conservation. Oxford University Press, Oxford, 383–410.

Jörgensen TL, Martin EC, Burt AJ (2015) Spatial variability in habitat structure and heterogenic coral reef fish assemblages inside a small-scale marine reserve after a coral mass mortality event. Ocean & Coastal Management 114: 32–41.

Kingsford MJ, Leis JM, Shanks A, Lindeman KC, Morgan SG, Pineda J (2002) Sensory environments, larval abilities and local self-recruitment. Bulletin of Marine Science 70(1): 309–340.

Mascarelli A (2014) Climate-change adaptation: designer reefs. Nature 508: 444–446. doi: 10.1038/508444a

Mbije NE, Spanier E, Rinkevich B (2013) A first endeavour in restoring denuded, post-bleached reefs in Tanzania. Estuarine, Coastal and Shelf Science 128: 41–51. doi: 10.1016/j.ecss.2013.04.021

Montoya-Maya PH, Macdonald AHH, Schleyer MH (2014) Estimation of size at first maturity in two South African coral species. African Journal of Marine Science 36(4): 513–516. doi: 10.2989/1814232X.2014.980848

Nakamura M, Sakai K (2009) Spatiotemporal variability in recruitment around Iriomote Island, Ryukyu Archipelago, Japan: implications for dispersal of spawning corals. Marine Biology 157(4): 801–810. doi: 10.1007/s00227-009-1363-2

Normile D (2009) Bringing coral reefs back from the living dead. Science 325(5940): 559–561. doi: 10.1126/science.325_559

Obura D (2005) Resilience and climate change: lessons from coral reefs and bleaching in Western Indian Ocean. Estuarine, Coastal and Shelf Science 63: 353–372.

O'Leary JK, Potts DC (2011) Using hierarchical sampling to understand scales of spatial variation in early coral recruitment. Coral Reefs 30: 1013–1023.

Petersen D, Laterveer M, Schumacher H (2005) Innovative substrate tiles to spatially control larval settlement in coral culture. Marine Biology 146(5): 937–942. doi: 10.1007/s00227-004-1503-7

Pratchett MS, Hoey AS, Wilson SK (2014) Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. Current Opinion in Environmental Sustainability 7: 37–43. doi: 10.1016/j.cosust.2013.11.022

R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Richmond RH, Hunter CL (1990) Reproduction and recruitment of corals: comparisons among the Caribbean, the Tropical Pacific, and the Red Sea. Marine Ecology Progress Series 60: 185–203. doi: 10.3354/meps060185

Rinkevich B (1995) Restoration strategies for coral reefs damaged by recreational activities: the use of sexual and asexual recruits. Restoration Ecology 3(4): 241–251. doi: 10.1111/j.1526-100X.1995.tb00091.x

Rinkevich B (2008) Management of coral reefs: we have gone wrong when neglecting active reef restoration. Marine Pollution Bulletin 56(11): 1821–1824. doi: 10.1016/j.marpolbul.2008.08.014

Schmidt-Roach S, Miller KJ, Woolsey E, Gerlach G, Baird AH (2012) Broadcast Spawning by *Pocillopora* Species on the Great Barrier Reef. PLoS ONE 7: 1–7.

Shackelford N, Hobbs RJ, Burgar JM, Erickson TE, Fontaine JB, Laliberté E, Ramalho CE, Perring MP, Standish RJ (2013) Primed for change: developing ecological restoration for the 21st century. Restoration Ecology 21(3): 297–304. doi: 10.1111/rec.12012

Skaug H, Fournier D, Nielsen A, Magnusson A, Bolker B (2012) Generalized Linear Mixed Models using AD Model Builder. R Package Version 0.7 2.

Spalding MD, Jarvis GE (2002) The impact of the 1998 coral mortality on reef fish communities in the Seychelles. Marine Pollution Bulletin 44: 309–321.

Spencer T, Teleki KA, Bradshaw C, Spalding MD (2000) Coral bleaching in the southern Seychelles during the 1997–1998 Indian Ocean warm event. Marine Pollution Bulletin 40(7): 569–586. doi: 10.1016/S0025-326X(00)00026-6

Sponaugle S, Cowen RK, Shanks A, Morgan SG, Leis JM, Pineda J, Boehlert GW, Kingsford MJ, Lindeman KC, Grimes C, Munro JL (2002) Predicting self-recruitment in marine populations: biophysical correlates and mechanisms. Bulletin of Marine Science 70: 341–375.

Suding K, Higgs E, Palmer M, Callicott JB, Anderson CB, Baker M, Gutrich JJ, Hondula KL, LaFevor MC, Larson BMH, Randall A, Ruhl JB, Schwartz KZS (2015) Committing to ecological restoration. Science 348(6235): 638–640. doi: 10.1126/science.aaa4216

Suzuki G, Hayashibara T, Shirayama Y, Fukami H (2008) Evidence of species-specific habitat selectivity of *Acropora* corals based on identification of new recruits by two molecular markers. Marine Ecology Progress Series 355: 149–159.

Underwood AJ (1993) The mechanics of spatially replicated sampling programmes to detect environmental impacts in a variable world. Australian Ecology 18(1): 99–116. doi: 10.1111/j.1442-9993.1993.tb00437.x

Vermeij MJA (2005) Substrate composition and adult distribution determine recruitment patterns in a Caribbean brooding coral. Marine Ecology Progress Series 295: 123–133. doi: 10.3354/meps295123

Veron JEN (2000) Corals of the World. Australian Institute of Marine Science, Townsville, 1382 pp.